

FOSSIL LIZARDS FROM THE EARLY PLIOCENE BLUFF DOWNS LOCAL FAUNA

by BRIAN S. MACKNESS¹ & MARK N. HUTCHINSON²

Summary

MACKNESS, B. S. & HUTCHINSON, M. N. (2000) Fossil lizards from the Early Pliocene Bluff Downs Local Fauna. *Trans. R. Soc. S. Aust.* **124**(1), 17–30. 31 May, 2000.

The lizard fauna of the Early Pliocene Bluff Downs Local Fauna consists of members of the families Scincidae, Gekkonidae, Agamidae and Varanidae. At least three living scincid taxa, *Egernia hosmeri*, *Tiliqua sinuoides* and a member of the *Eulamprus quoyii* complex, have been identified from dentary, maxillary and skull roof elements. The gekkonids are represented by a nearly complete dentary, which is tentatively referred to the living genus *Heteronotia*. Agamids are represented by unidentified dentary remains. A giant varanid, *Megalania* sp., was the only extinct lizard found; other smaller varanid remains were also recovered. The gekkonid is the first published Pliocene record of the family from Australia. The fauna, consisting largely of taxa with close phyleric links to the modern lizard fauna of eastern Australia, is a further example of the evolutionary conservatism of Australian herpetological assemblages since the Miocene.

KEY WORDS: Pliocene, Bluff Downs Local Fauna, lizards, *Egernia*, *Tiliqua*, *Eulamprus*, *Heteronotia*, *Megalania*, varanids.

Introduction

Squamates are poorly represented in the Australian fossil record (Molnar 1982, 1984a,b, 1985, 1991). The few records older than the K-T boundary (Bartholomai 1979) are suspect, as the groups to which they were assigned (Paliguaniidae and Proactertiformes) are now thought to be non-squamate or, at best, of uncertain affinities. Molnar (1985) reported that vertebrae of a small lepidosaur (possibly a sphenodontid) had been found in the Cretaceous Toolebuc Formation of Queensland. Some fragmentary remains of 'lizards' including a rib (Flannery & Rich 1981), a humerus (Molnar 1980) and an incomplete maxillary (or dentary) (Molnar 1985) have yet to be fully described. A supposed lizard jaw from the early Cretaceous Dinosaur Cove has proven to be a fish (Molnar & Czechura 1990).

The earliest Australian Tertiary lizard mentioned in the literature (based on a submitted manuscript cited in Rich *et al.* 1991) is from the Eocene Tingamarra Local Fauna (Molnar 1991). Now published, this paper (Godthelp *et al.* 1992) reports no lizards. Unpublished data do exist to indicate the presence of squamates at the site (MNH, pers. obs.) but the remains are at present, too few and fragmentary to reach conclusions regarding their relationships to the

living fauna. The first confirmed record of lacertilians with modern day counterparts comes from the Oligo-Miocene deposits of central Australia (Stirton *et al.* 1967 (this record is actually of a snake vertebra) (see Estes 1984) (Estes 1984; Pledge 1984). The Miocene limestone deposits of the Riversleigh area of north-western Queensland are known to contain fossils of agamids, varanids, gekkonids and scincids (Archer *et al.* 1989, 1991; Covacevich *et al.* 1990; Hutchinson 1992; Shea & Hutchinson 1992).

Pliocene records of lizards include *Varanus* sp. indent. and *Tiliqua* sp. from the Curramulka Local Fauna (Pledge 1992), *Tiliqua* sp. from Wellington Caves (Hand *et al.* 1988), *Megalania* sp. from the Chinchilla Local Fauna (Hecht 1975) and a lizard from the Bow Local Fauna (Skilbeck 1980). Archer (1976) reported an agamid and *Varanus* sp. from the Early Pliocene Bluff Downs Local Fauna. A number of non-squamatan taxa has been previously reported from this fauna (Archer 1976, 1982; Bartholomai 1978; Archer & Dawson 1982; Rich & van Tets 1982; Boles & Mackness 1994; Mackness 1995 a,b; Willis & Mackness 1996; Thomson & Mackness 1999; Wroe & Mackness 1999). The present paper describes the lizards identified to date and discusses the implications for palaeoecology of the site and the pattern of lizard evolution in Australia.

Materials and Methods

Fossil remains of reptiles were obtained through quarrying or through wet-sieving of sediments.

¹School of Biological Sciences, University of New South Wales, Kensington NSW 2052. Present address: PO Box 560 Buerwah QLD 4519. E-mail: megalanina@compuserve.com
²Department of Herpetology, South Australian Museum North Terrace Adelaide SA 5000.

TABLE 1. Measurement (mm) of dorsal ?*Megalania vertebrae* against *Varanus giganteus* vertebrae. Measurements as defined in Methods. Range (mean \pm standard deviation). Data for *V. giganteus* are taken from Smith (1976).

Specimen	No	Pr-Po	BW /Pr-Po	CW/Pr-Po	Pr-Pr/Pr-Po
<i>V. giganteus</i>	20	24.5-27.1 (25.7 \pm 1.4)	0.54-0.64 (0.58 \pm 0.05)	0.55-0.63 (0.59 \pm 0.06)	0.88-1.01(0.92 \pm 0.07)
Fossil	7	31.7-45.8 (36.4 \pm 5.3)	0.48-0.57 (0.53 \pm 0.04)	0.56-0.72 (0.63 \pm 0.06)	1.07-1.21(1.14 \pm 0.06)

TABLE 2. Measurements (mm) of individual ?*Megalania vertebrae*. Measurements as defined in Methods. (Mean \pm standard deviation).

Specimen	Pr-Po	Pr-Pr	Po-Po	BW	CW	Type
F9135	31.7	38.2	34.5	15.9	19.9	Dorsal
F23234	40.0	46.5	42.5	22.0	25.9	Dorsal
F23235	33.7	-	-	-	-	Dorsal
F23236	32.1	-	32.0	16.8	-	Dorsal
F23237	32.7	35.8	-	15.7	19.9	Dorsal
F23681	38.9	41.8	-	22.3	21.8	Dorsal
F23686	45.8	53.5	-	25.7	32.9	Dorsal
F23684	38.3	-	29.0	-	14.3	Cervical
(Mean/SD)	(36.4 \pm 5.31)	(43.2 \pm 7.05)	(36.3 \pm 5.48)	(19.7 \pm 4.2)	(24.1 \pm 5.51)	

Specimens were examined using a Wild M3Z stereomicroscope with eyepiece micrometer and drawing tube. X-ray microanalysis was carried out using a JEOL JSM 35 scanning electron microscope and energy dispersive X-ray detector. Terminology for bones follows Ramer (1956).

Measurements

Measurements made using vernier calipers accurate to 0.05 mm are summarised below and largely follow Smith (1976). Statistical analysis of these measurements is provided in Tables 1 & 2.

VERTEBRAL LENGTH (PR-PO) - measured as the greatest distance from the anterior edge of the prezygapophysis to the posterior edge of the postzygapophysis.

PREZYGAPOPHYSIAL WIDTH (PR-PR) - measured as the greatest distance between the edges of the prezygapophyses.

POSTZYGAPOPHYSIAL WIDTH (PO-PO) - measured as the greatest distance between the edges of the postzygapophyses.

CENTRUM MINIMUM WIDTH (BW) - measured as the smallest distance across the centrum.

CONDYLAR WIDTH (CW) - measured as the greatest distance between the condyle.

Abbreviations for specimen numbers: QM 1; Queensland Museum fossil numbers; SAMA, South Australian Museum, Adelaide; AR, University of New South Wales Research Collection. Site localities are listed in Archer & Wade (1976) and Mackness (unpub.).

Systematics

Family Gekkonidae Gray, 1825

Subfamily Gekkoninae Underwood, 1954

cf. *Heteronotia* sp. (Gray, 1845)
(FIG. 1A)

Material examined: A single nearly complete left dentary (QM F23655) from EVS Site.

Characters

Gekkonid dentition is characterised as isodont with a large number of cylindrical, pointed teeth confined to the marginal bones (Edmund 1969). Sumida & Murphy (1987) have amended this by reporting that gekkonoids typically have bicuspid tooth crowns, the cusps being separated by an apical groove. Allocation of this specimen to *Heteronotia* is justified below.

Description

The specimen is an almost complete left dentary, complete anterior to the level of the posterior end of the tooth row and retaining most of the angular process. There are 36 teeth or tooth loci. The jaw is relatively slender and curves mesially at about the level of the 18th tooth. Meckel's groove is completely obliterated by dentary overgrowth. The internal septum is not exposed by the splenial notch, which extends anteriorly to the level of the 29th tooth,

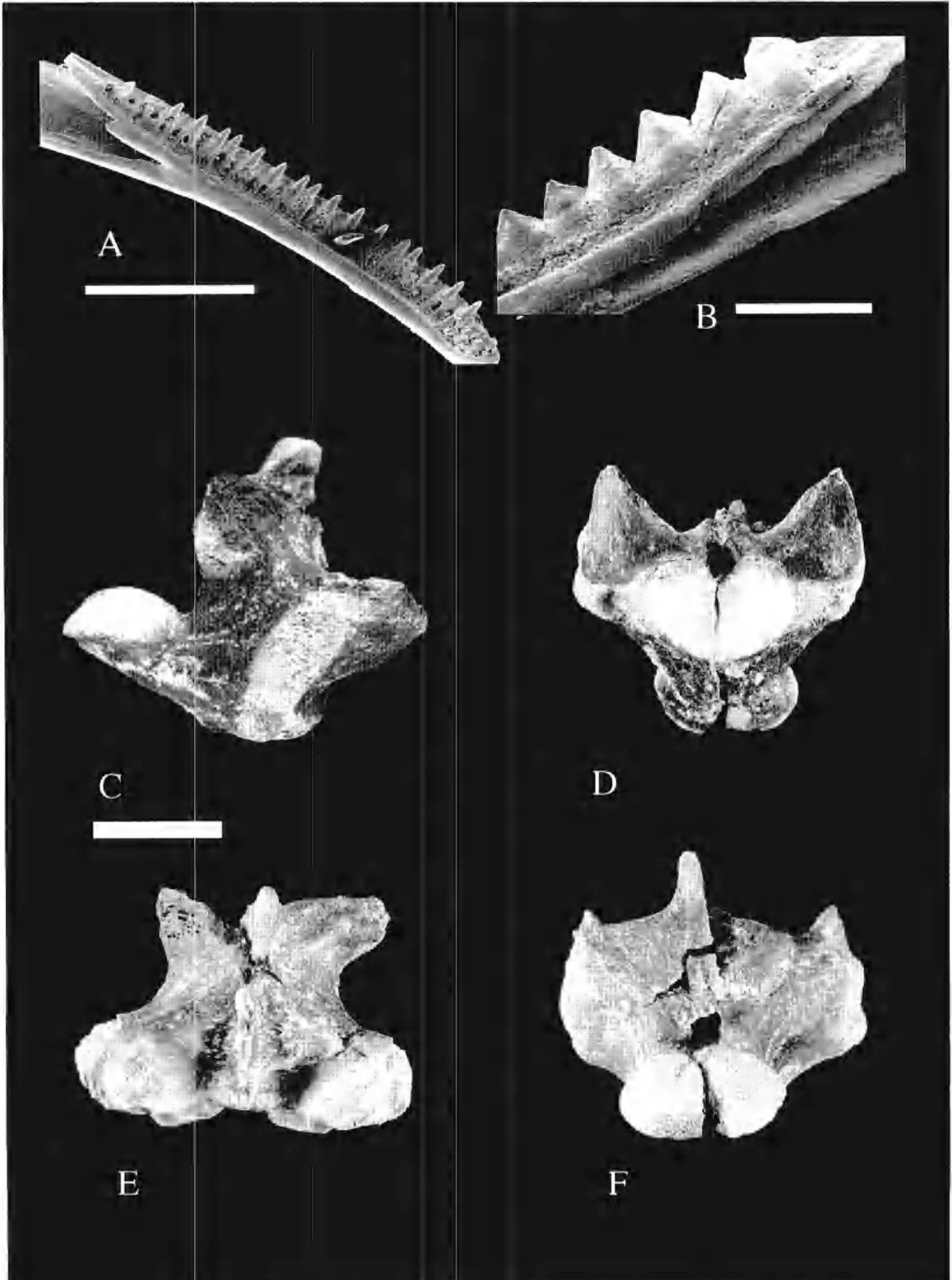


Fig. 1 (A). cf. *Heteronotia* sp. QM F23655 left dentary, lingual. Scale bar = 2 mm. (B). Agamid indented. QM F7812 dentary, lingual. Scale bar = 1 mm. (C-F). ?*Megalania* sp. QM F23686, dorsal vertebra. (C). Lateral. (D). Anterior. (E). Dorsal. (F). Posterior. Scale bar = 20 mm.

The teeth are delicate, sharply pointed and weakly bicuspid, with a lingual cusp set off by a groove and lying lower than the apical cusp. There is little variation in tooth size apart from a slight diminution posteriorly. The dental sulcus is well demarcated by a lingual parapet. Labially, the jaw bears four widely-spaced mental foramina, the most posterior level with the 25th tooth.

Dimensions

Jaw depth (at the level of the posterior most tooth), 2.6 mm; length of tooth row, 12 mm; height of 14th tooth, 0.4 mm.

Remarks

The dentaries of gekkonids are conservative, making identification difficult. Pygopods have highly variable and specialised jaws (Hutchinson 1997), none of which strongly resembles the specimen described. Most of the larger carphodaetylines have distinctive, tapering multi-toothed (> 40) dentaries quite unlike this specimen. However most diplodaetylines and the Australian gekkonines have less specialised jaws which are superficially similar to each other. Of the genera examined (all Australian gekkonoids except *Pseudothecadactylus* (= *Rhacodaetylus*)), the most similar to QM F23655 is *Heteronotia*. At present, this attribution is based only on the combination of jaw proportions, tooth number and size; objective criteria for most gekkonid jaws have still to be developed.

Heteronotia binocci (Gray, 1845) is a wide ranging complex of at least two bisexual species and numerous all-female parthenogenetic clones. Members of the complex are found throughout mainland Australia (Moritz 1983; Moritz *et al.* 1989) in a variety of habitats ranging from deserts to closed forests. *Heteronotia binocci* is nocturnal and feeds on arthropods (Bustard 1968, 1970). The relationships of the two other species, *H. spelea* (Kluge, 1963) and *H. planiceps* Storr, 1989 to the known chromosome races and to each other are yet to be clarified. Pending the clarification of species boundaries, we can make no firmer allocation of the fossil specimens than as a possible *Heteronotia* species.

Fossil gekkonids have also been recorded from the Quaternary of Queensland (Archer 1978)

Family Agamidae Gray, 1827

Unidentified Material (FIG. 1B)

Material examined. Two fragmentary right dentaries, the symphyseal region of the jaw (QM

F23656) EVS site, the other (QM F7812), a partial dentary bearing the mid-to-rear section of the tooth row from Main Site.

Characters

Agamid reptiles are distinguished by having a dentition combining one to three anterior pleurodont teeth followed by acrodon teeth. Other agamid features are summarised by Estes (1983).

Description

Both specimens are from relatively moderate-sized individuals. The partial right dentary (QM F7812) bears seven acrodon teeth. The last implanted tooth is followed by an empty locus. The dentary is broken anteriorly at what is estimated to have been about the mid-point of the tooth row.

The second specimen, (QM F23656), is the symphyseal region of a right dentary. It bears two pleurodont tooth loci (one tooth present, one absent), followed by five partly damaged acrodon teeth. Three closely-spaced mental foramina are preserved on the labial surface of the specimen, the third being situated below the first acrodon tooth.

Dimensions

Jaw length (QM F7812), 7.8 mm; (QM F23656), 5.9 mm.

Remarks

Archer (1976) suggested that the small right dentary (QM F7812) was similar to some species of *Amphibolurus*. Since that time, the generic classification of Australian agamids has been considerably revised (e.g. Storr 1982) and further review of the phylogeny of the Australian dragons is likely (Greer 1989). Covacevich *et al.* (1990) identified several problems in identifying agamid remains and we follow their caution in not identifying these dentary fragments past family level.

Dragon lizards are divided into three lineages within Australia: the amphibolurids (*sensu* Hutchinson & Donnellan 1993), *Hypsilurus* and *Physignathus*. The amphibolurids inhabit nearly all environments except wet forests (Hutchinson & Donnellan 1993). *Physignathus* occurs along streams in a variety of habitats while *Hypsilurus* is restricted to closed canopy forests (Witten 1993).

Fossil agamids have been recorded from the Quaternary of Queensland (Bennett 1876; Archer 1978; Archer & Braysbaw 1978), New South Wales (Ryder 1974; Dodson *et al.* 1993; Balme 1995) and South Australia (Hale & Tindale 1930; Hope *et al.* 1977; Smith 1976, 1982; Smith 1982; Pledge 1990).

Family Varanidae Gray, 1827

?*Megalania* sp.
(FIGS 1C-E, 2A-C)

Material examined: Two isolated cervical vertebrae (QM F23684) JHY Site, (QM F23233) Main Site, seven isolated dorsal vertebrae (QM F9135, QM F23234, QM F23235, QM F23236, QM F23237) Main Site; (QM F232686, QM F232687) DML Site and condyle fragments (QM F23688).

Characters

Megalania is characterised, in part, by having massive thoracic and lumbar vertebrae with weakly developed zygosphenes (absent in typical *Varanus*) as well as small depressed neural canals. The adult teeth of *Megalania* are large and slightly recurved distally. The anterior cutting edge is rounded and serrated distally. The posterior cutting edge is thin, blade-like and serrated along its entire length (Hecht 1975).

Description

The two isolated fossil cervical vertebrae are similar in overall morphology to those from an extant *Varanus varius* (White, 1790) (AR7641) but are some 22% larger. Both fossil vertebrae lack neural spines but bear hypapophyses with the grooved, knob-like extremities characteristic of large-sized varanids. The cotyle is more robust and less flattened than that of the extant species and the condyle is less ovate. Both these features may be allometric in nature, however. The dorsal vertebrae are much more massive than those of any extant varanid. Tables 1 & 2 summarise the measurements of the ?*Megalania* vertebrae. The animal represented was clearly larger than modern varanid counterparts such as the perentie *Varanus giganteus* with the largest dorsal vertebra being almost 70% larger than those measurements supplied for a perentie by Smith (1976).

Remarks

The assignment of the larger varanid vertebrae to *Megalania* is made on the basis of convention. *Varanus* and *Megalania* are the two genera recognised from Australia, but the two are separated primarily on size. Estes (1983) doubts whether the two ought to be generically distinct. *Megalania prisca* Owen, 1860 is the only species currently recognised and is significantly larger than all extinct and extant varanids. Large varanid vertebrae are also known from the Chinchilla Local Fauna (Hecht 1975) and these along with those from Bluff Downs are currently being studied by one of the authors

(B.M.). Hecht (1975) in his study of *M. prisca* noted that there seemed to be fewer caudal and cervical vertebrae associated with remains of *Megalania* compared with the expectation based on *Varanus*. This suggested to him that *Megalania* may have had a proportionally shorter neck and tail than extant varanids. No caudals have been recovered from the large varanid from Bluff Downs.

Varanus sp.
(FIG. 2D-I)

Material examined: Isolated dorsal vertebrae (QM F7774, QM F23238, QM F23659) Main Site; (QM F23683) EVS Site; isolated caudal vertebrae (QM F7777, QM F9131) Main Site; (QM F23681, QM F23682) EVS Site; and isolated teeth (QM F23685).

Characters

Varanids are recognised by having vertebrae characterised by oblique condyle-cotyler articulations, particularly in the thoracic and lumbar region with the vertebral centra constricted anterior to the condyles. The bases of the teeth are expanded and sculptured with fine vertical fluting (Fejervary 1935; McDowell & Bogert 1954; Romer 1956; Hoffstetter & Gase 1969; Hecht 1975).

Description

The dorsal vertebrae show characteristic varanid morphology and with a range of centra lengths (Table 3) which indicate a medium-sized goanna such as *Varanus gouldii* (Gray, 1838).

TABLE 3. Measurements (mm) of centra of fossil varanids and *Varanus varius* (AR7641).

	Dorsal	Cervical
QM F7774	14.2	QM F9131 22.6
QM F23683	13.8	QM F23681 18.2
QM F23659	10.8	QM F23682 15.7
QM F23238	10.5	QM F7777 10.9
AR7641(a)	15.3	
AR7641(b)	15.3	
AR7641(c)	15.4	
AR7641(d)	15.4	
AR7641(e)	15.6	
AR7641(f)	15.7	

Remarks

Given that there appears to be a narrow range of measurement within the dorsal section of the vertebral column of individual goannas and that there are two distinct size classes of fossil dorsal vertebrae, it is reasonable to assume that either two

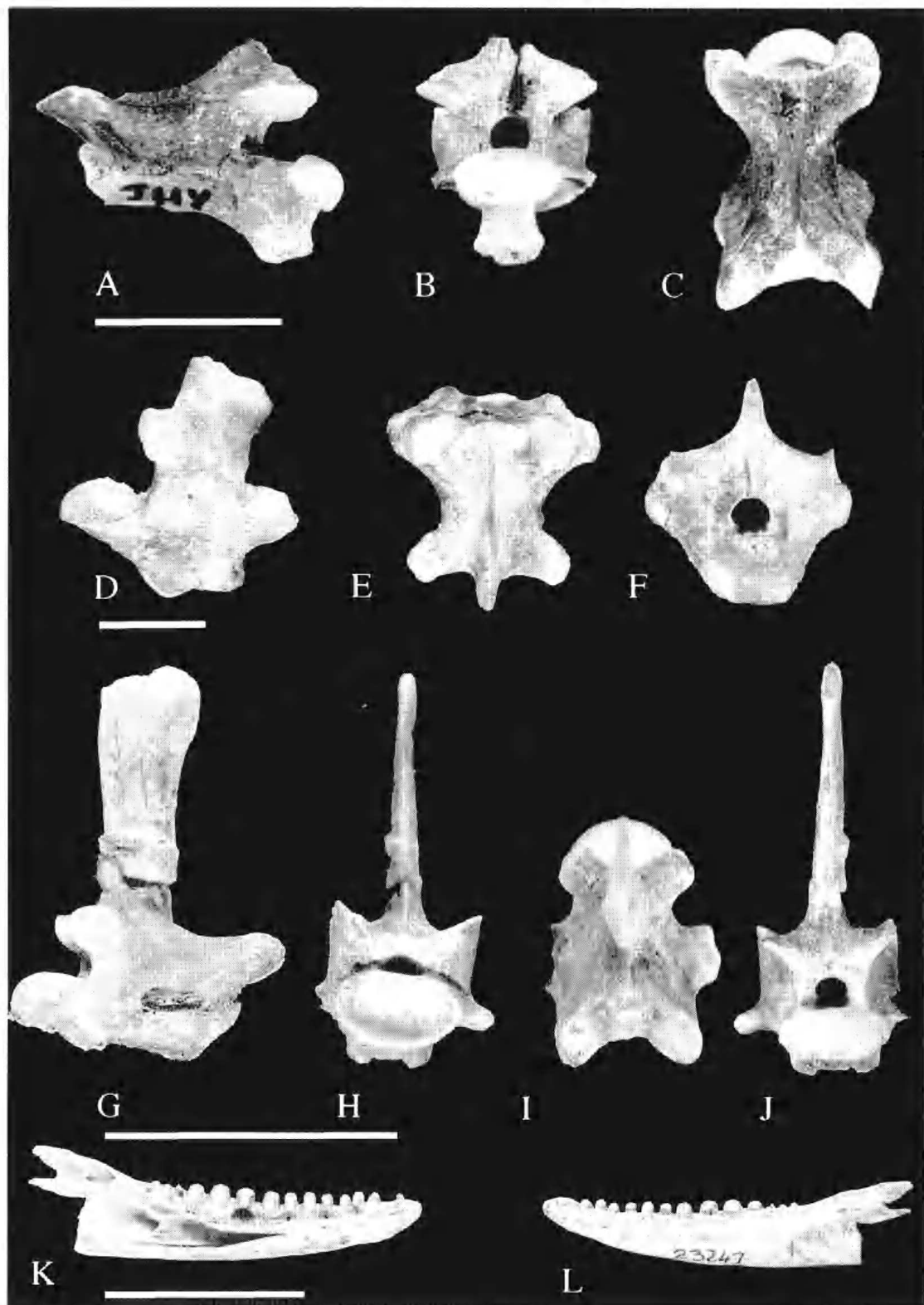


Fig. 2 (A-C). *?Megalania* sp. QM F23686 cervical vertebra. (A). Lateral. (B). Posterior. (C). Dorsal. Scale bar = 40 mm. (D-F). *Varanus* sp. QM F7774 dorsal vertebra. (D). Lateral. (E). Dorsal. (F). Posterior. Scale bar = 10 mm. (G-J). *Varanus* sp. QM F9131 caudal vertebra. (G). Lateral. (H). Anterior. (I). Dorsal. (J). Posterior. Scale bar = 50 mm. (K-L). *Tiliqua scincoides* QM F23247 left dentary. (K). Lingual. (L). Labial. Scale bar = 20 mm.

sympatric species or two size morphs are represented in the fauna. The caudal vertebrae show a much wider range of measurements which is typical of this section of the vertebral column. Once again however, two size classes can be inferred indicating that either two sympatric species or two size morphs are present. Only one of the caudal vertebrae (QM F9131) has a complete neural spine.

Mertens (1942) suggested a relationship between body length and tail length which Hecht (1975) further extrapolated, suggesting that the long tails of some varanids may be a reason for the disparate appearance of caudal vertebrae over those from other regions of the body in the fossil record. An equal number of dorsal and caudal varanid vertebrae has been recovered from Bluff Downs. Wilkinson (1995) has recently listed a number of vertebral features for different *Varanus* species. Although potentially useful, these characters have been selected from single isolated specimens and therefore cannot take into account interspecific and intraspecific variation in varanid vertebral characters. It is not possible to identify the fossil vertebrae beyond *Varanus* sp., partly due to the current lack of information and because the vertebrae recovered were not articulated and were possibly from several individuals. The vertebrae also came from two different sites, even though those sites are from comparable depositional sequences (Mackness unpub.). The size of the animal cannot be extrapolated from the vertebrae given the problems identified above as well as those identified by Hecht (1975).

Varanids are found over a wide range of habitats including aquatic, terrestrial and arboreal and from tropical forests to arid deserts (Cogger & Heatwole 1981). They range over a wide area and eat most food items including invertebrates, vertebrates and carrion (King & Green 1979, 1993 a,b; Losos & Greene 1988; James *et al.* 1992).

Fossil varanids are known from the Quaternary of Queensland (Archer 1978; Walters 1980; Hope 1981; Horton 1981; Wilkinson 1995), New South Wales (Tedford 1967; Aplin quoted in Hope 1981), South Australia (Hale & Tindale 1930; Mulvaney *et al.* 1964; Smith 1976, 1982; Smith 1982; Hope *et al.* 1977; Williams 1980; Pledge 1990) and Western Australia (Archer 1977).

Family Scincidae Gray, 1825

Subfamily Lygosominae Mittleman, 1952

Tiliqua Gray, 1825

Tiliqua scincoides (White, 1790)

(FIG. 2 K-L)

Material examined: Almost complete left dentary (QM F23247) EVS Site.

Characters

The closed Meckelian groove and the presence and form of several large hemispherical-conical cheek teeth uniquely characterise this as belonging to the genus *Tiliqua* (Shea & Hutchinson 1992).

Description

The specimen is left dentary minus angular process, a vertical broken edge runs just posteriorly to the level of the internal facet for the dentary process of the coronoid bone, but the complete, posteriorly projecting coronoid process of the dentary is still present. Sixteen teeth or alveoli are present, cheek teeth increasing in size posteriorly with the largest being the 11th, 12th and 13th, after which last three are abruptly smaller. A buttress supporting the mandibular symphysis rises abruptly below the dentary as a low keel at about the level of the 6th tooth, visible as a fold running posteriorly along the ventral face of the dentary to about the level of the anterior alveolar foramen. The anterior end of this foramen, that is, the apex of the splenial notch, is at the level of the 10th tooth.

The crowns of the enlarged cheek teeth are markedly wider than the tooth bases, with almost horizontal flattened peripheral occlusal surfaces rising to a central point. Striae radiate over the occlusal surface from this central point.

Measurements

Tooth row length 22 mm; jaw depth at level of last tooth 9.5 mm.

Remarks

The *Tiliqua* dentary was found lying on top of the ground at EVS Site, in an area undisturbed by quarrying. Fossils are often exposed at the Bluff Downs site through rain and other disturbances. The colour of this particular dentary was different from others recovered from the site, raising doubt about its provenance. X-ray microanalyses of mineral content (Figs 1-4) were undertaken on the *Tiliqua* jaw from EVS Site, an extant *Tiliqua*, as well as on fossil bone fragments of a turtle and a python, both from EVS Site.

The results of these microanalyses showed that silica was a prominent constituent of the fossil bones, whereas in the extant *Tiliqua*, little silica was present. Since the calcium phosphate of the bone is often changed by the addition or substitution of other minerals, such as silica, during fossilisation, these results indicate that the *Tiliqua* jaw from EVS Site was fossilised and probably contemporaneous with the other reptiles sampled.

The Bluff Downs specimen is not distinguishable from the living *T. scincoides* and at least one other Pliocene *Tiliqua*, reported by Pledge (1992) from

Currumulka, can also be allocated to this species. Examination of these specimens (partial dentary, maxilla and frontal) by MNH shows them to be indistinguishable from those of the living species. However, another much larger specimen referable to *Tiliqua*, recently discovered from the Pliocene Chinchilla Local Fauna (Hutchinson & Mackness unpub.), is markedly different from any living or extinct species of the genus.

Tiliqua scincoides and its sister species *T. gigas* (Schneider, 1801) (Shea 1990) are the most tropical and forest-adapted members of this genus. *Tiliqua scincoides* is an adaptable species, found in a wide variety of habitat types and its presence does not have strong palaeoecological implications.

Egernia Gray, 1838

Egernia hosmeri Kinghorn, 1955
(FIG. 3A)

Material examined: A partial right maxillary fragment (QM F23654) EVS Site.

Characters

The maxillary is identified as a spiny-tailed skink (*E. cunninghami* (Gray, 1832) group (*sensu* Horton 1972)) on the basis of its tooth morphology having compressed crowns with occlusal blades oriented such that the teeth in the jaws form a serrated cutting edge.

Description

The specimen is the posterior, suborbital portion of the right maxillary tooth row. The V-shaped notch for the jugal is almost complete as is the dorsal edge (orbital rim). Posterior nine teeth or tooth loci are preserved. The crowns of more intact teeth are labiolingually compressed, with angular occlusal cutting edges. Crowns are also somewhat flared in lingual view, producing an overall 'ace-of-spades' shape. This tooth shape is limited to members of the *Egernia cunninghami* species group (Horton 1972) which comprises *E. cunninghami*, *E. depressa* (Günther, 1875), *E. hosmeri* and *E. stokesii* (Gray, 1845).

The four living members of this species group differ in the details of their dentition: *Egernia cunninghami* and *E. depressa* have squared-off, somewhat chisel-shaped crowns. *Egernia stokesii* and *E. hosmeri* show the greatest similarity to each other and to QM F23654, all three having teeth with linguo-labially flattened crowns which rise to a medial point. SAMA specimens of *E. stokesii* differ slightly from those of *E. hosmeri* in being rather more flared in lingual view, this expansion being true even of the most posterior teeth. In *E. hosmeri* and QM F23654 the last few teeth are narrower and more acutely pointed than those of *E.*

stokesii. The fossil is not distinguishable from *T. hosmeri* and is therefore allocated to that species.

Measurements

Length of specimen, 6.9 mm; depth at level of jugal suture, 2.1 mm; height of largest tooth, 1.7 mm.

Remarks

Spiny-tailed skinks are all crevice dwellers, typically in rock outcrops but sometimes also in logs and stumps. The better studied species (*E. cunninghami* and *E. stokesii*) are almost entirely herbivorous in the wild (Brown 1991).

Eulamprus Fitzinger, 1843

Eulamprus quoyii complex
(FIG. 3C-F)

Material examined: A right dentary (QM F9137) Main Site. A frontal (QM F23657) Main Site and several other fragments (QM F23658) AB Site are possibly also referable to this taxon.

Characters

Eulamprus comprises the larger, more generalised members of the *Sphenomorphus* Group (Greer 1979) in Australia. Its definition is currently based mainly on scalation and reproductive characters, but initial work (Hutchinson 1992) shows that by using tooth crown morphology as well as jaw robustness at least two morphological groups are recognisable osteologically, the more gracile water skinks, *E. quoyii* (Dumeril & Bibron, 1839) and its relatives, and the more robust tropical forest species such as *E. murrayi* (Boulenger, 1887).

Description

The dentary is nearly complete, with a tooth row bearing 24 teeth or tooth loci. The dental sulcus is demarcated lingually by a pronounced parapet which diminishes and disappears at about the level of the 22nd tooth. Meckel's groove is widely open along the ventrolingual face of the dentary. The internal septum of the dentary is poorly developed and does not show much posterior extension. Seven mental foramina are present, the last at about the level of the 19th tooth. The teeth crowns are not flared or thickened. The lingual face of each tooth crown is vertical, with an inward-projecting buttress offset to the rear. The junction of the lingual face of the tooth crown with the occlusal surface is demarcated by a groove which separates two closely apposed low ridged edges.

Measurements

Length of tooth row, 12 mm; depth of dentary at level of the 20th tooth, 2.6 mm.

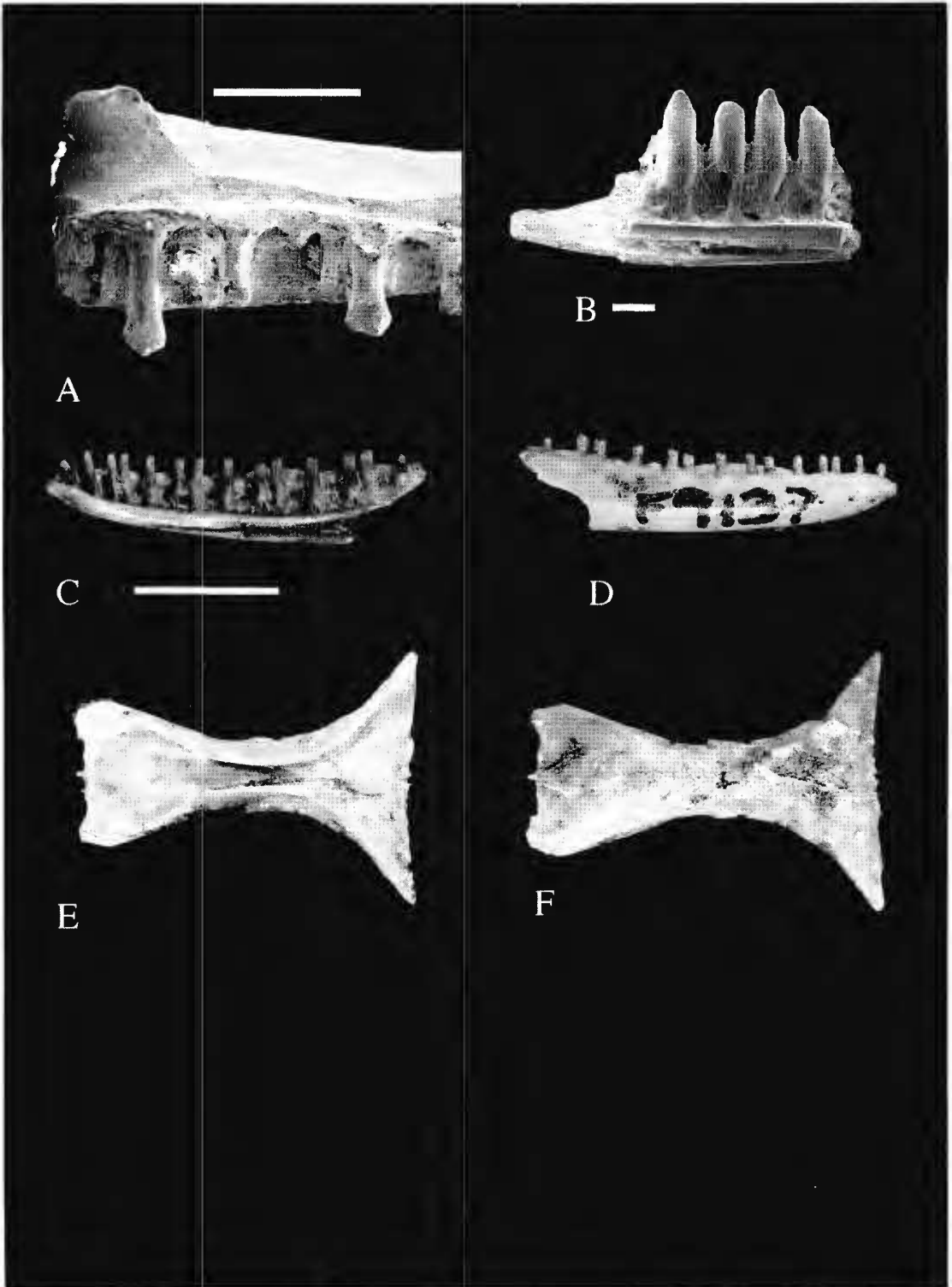


Fig. 3. (A). *Egernia hosmeri* QM F23654 right maxillary fragment. Scale bar = 2 mm. (B). Scincidia indent. QM F23659. Scale bar = 1 mm. (C-D). *Eulamprus quoyii* complex QM F9137 right dentary. (C). Lingual. (D). Labial. Scale bar = 20 mm. (E-F). *E. quoyii* complex. QM F23657 frontal. (E). Ventral. (F). Dorsal. Scale bar = 20 mm.

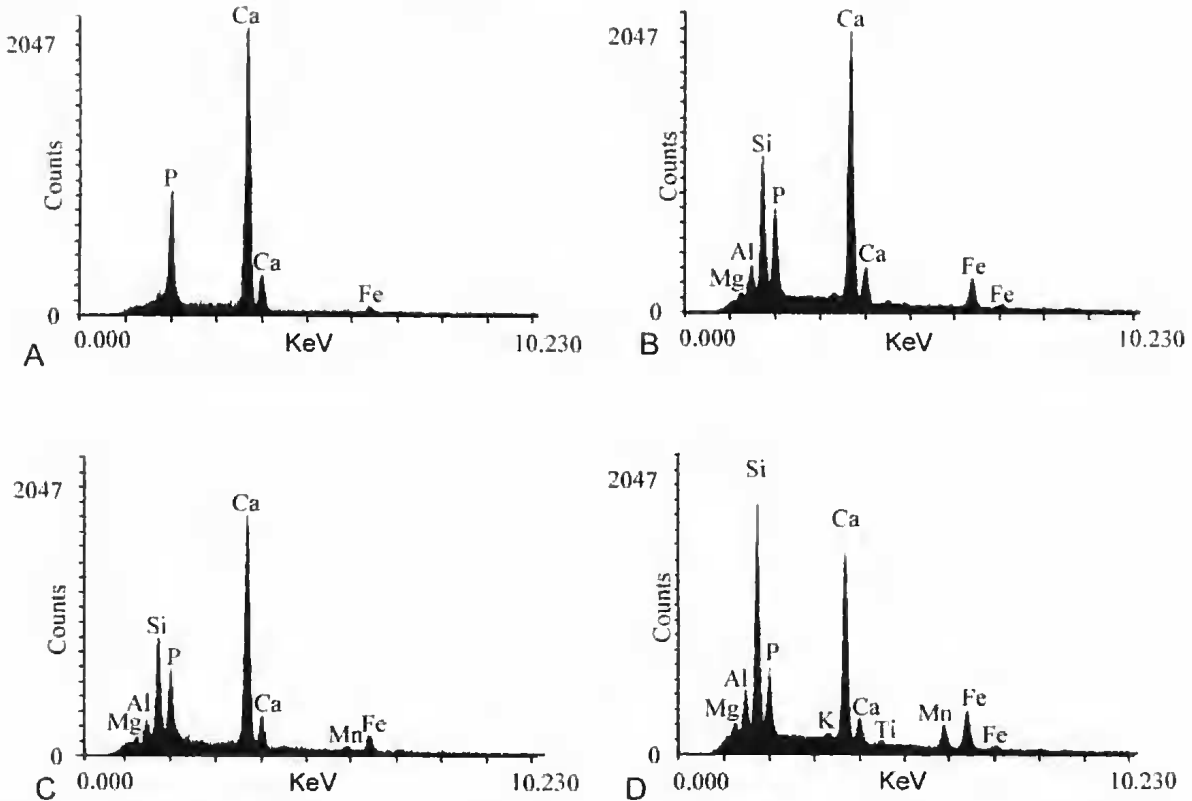


Fig. 4. X-ray microanalysis of bone. (A). Recent *Tiliqua scincoides* dentary. (B). Fossil *T. scincoides* dentary. (C). Fossil turtle shell. (D). Fossil python vertebra.

Remarks

This specimen is very similar to living water skinks and is clearly distinct from the more robust rainforest *Eulamprus* spp. such as *E. murrayi* in that it lacks their deep jaws and somewhat large, durophagous cheek teeth. However, the fossil appears to differ from *E. quoyii*, the living species in the area today. Specimens of *E. quoyii* of comparable jaw size have a longer, narrower dentary bearing up to 30 teeth. Thus, if this specimen were *E. quoyii*, it would have to be regarded as having an anomalously low tooth count. The proportions and the number of teeth accord better with *E. tympanum* (Linnberg & Andersson, 1913) and *E. heatwolei* (Wells & Wellington, 1984), both restricted today to south-eastern Australia.

Water skinks are largely confined to permanent water with this habit enabling them to inhabit a wide range of habitats. They are diurnal and carnivorous, feeding on invertebrate and small vertebrate prey (Daniels 1987; Brown 1991).

Scincidae indent. (FIG. 3B)

Material examined: Three fragments (QM F23658) EVS Site; one small fragment (QM F23659) AB Site and an isolated vertebra (QM F23660) Main Site.

Remarks

Four fragments of lizard dentary and a vertebra are not sufficient to be assigned. The three pieces from the larger skink compare well with members of *Eulamprus* and are tentatively assigned cf. *Eulamprus*. The other remaining fragment represents another type of skink but not enough remains for any generic assignment. The vertebra is identified as a scincid on the basis of characters outlined by Smith (1976).

Fossil skinks are known from the Quaternary of Queensland (Trezise 1970; Bartholomai 1977; Archer & Brayshaw 1978; Molnar 1978). New South Wales (Kreff 1867, 1870, 1871; Lampert 1971;

Thorne 1971; Marshall 1973; Ryder 1974; Dodson *et al.* 1993; Balme 1995). Tasmania (Bowdler 1974), South Australia (Stirling 1889; Hale & Tindale 1930; Tindale 1933; Mulvaney 1960; Mulvaney *et al.* 1964; Smith, 1976, 1982; Hope *et al.* 1977; Smith, 1982; Pledge 1990, 1992;) and Western Australia (Cook 1960, 1963; Balme *et al.* 1978).

Discussion

The paucity of information about lizards in the Pliocene makes the Bluff Downs material particularly noteworthy. The fauna, in so far as it can be identified, is composed of species or species groups that occur in the modern Charters Towers area, the only obvious exception being the extinct *Megalania*. In this respect, the lizard fauna of the Bluff Downs Local Fauna is similar to the older Riversleigh deposits (Hutchinson unpub.) in that it represents an early establishment of modern forms in the area, contrasting with the contemporaneous mammal fauna which includes many extinct taxa.

Slow rates of faunal turnover, when compared with mammals, seem to be the rule in Tertiary and Quaternary squamates. This has been addressed most recently by the detailed study of the Rancho La Brea snakes by La Duke (1991). His explanation of low rates of extinction, evolution and faunal turnover in reptiles (compared with mammals and birds) centres on two concomitants of reptile ectothermy: - low energy requirements and small size enabling survival

of reptile populations in refugia too small for the rapidly metabolising and generally larger endotherms (witness the recent situation in Australia regarding mammal versus reptile extinctions). Thus, during periods of environmental change, many endotherm populations and species can be driven to extinction by habitat reduction, while the syntopic reptiles and amphibians merely suffer range contraction or fragmentation. Restoration of former climatic regimes permits re-establishment by the former reptile populations but may require evolutionary change or migration before a new mammal fauna emerges.

Acknowledgments

J. Mead and K. Aptin provided helpful comments on the manuscript. D. Sewell and L. Durham, School of Earth Sciences, University of Melbourne carried out the X-ray microanalysis. The Smith family of Bluff Downs Station continue to provide help and support for the ongoing research into the Bluff Downs Local Fauna. The collection of the Bluff Downs material was supported in part by an ARC Program Grant to M. Archer, a grant from the Department of Arts, Sport, the Environment, Tourism and Territories to M. Archer, S. Hand and H. Godthelp, a grant from the National Estate Program Grants Scheme to M. Archer and A. Bartholomai and grants in aid to the Riversleigh Research Project from Wang Australia, ICI Australia and the Australian Geographic Society.

References

- Archer, M. (1976) Bluff Downs local fauna. In Archer, M. & Wade, M. Results of the Ray E. Lemley Expeditions. Part I. The Allingham Formation and a new Pliocene vertebrate fauna from northern Australia. *Mem. Qld Mus.* **17**, 379-397.
- (1977) Appendix VIII. Faunal remains from the excavation at Puntutjarpa rockshelter pp. 158-165. In Gould, R. A. (Ed.) "Puntutjarpa rockshelter and the Australian desert culture" Anthropological Papers of the American Museum of Natural History, Volume 54.
- (1978) Quaternary vertebrate faunas from the Texas Caves of south-eastern Queensland. *Mem. Qld Mus.* **19**, 61-109.
- (1982) Review of the dasyurid (Marsupialia) fossil record, integration of data on phylogenetic interpretation and suprageneric classification pp. 397-443. In Archer, M. (Ed.) "Carnivorous marsupials" (Royal Zoological Society of New South Wales, Sydney).
- & BRAYSHAW, H. (1978) Recent local faunas from excavations at Hervey's Range, Kennedy, Jourama and Mount Roundback, north-eastern Queensland. *Mem. Qld Mus.* **18**, 165-177.
- & DAWSON, L. (1982) Revision of marsupial lions of the genus *Thylacoleo* Gervais (Thylacoleonidae, Marsupialia) and thylacoleonid evolution in the late Cainozoic pp. 477-494. In Archer, M. (Ed.) "Carnivorous marsupials" (Royal Zoological Society of New South Wales, Sydney).
- , GODTHELP, H., HAND, S. J. & MEGIRIAN, D. (1989) Fossil mammals of Riversleigh northwestern Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Aust. Zool.* **25**, 29-65.
- , HAND, S. J. & GODTHELP, H. (1991) "Riversleigh - the story of animals in ancient rainforests of inland Australia" (Reed, Sydney).

- & WADDE, M. (1976) Results of the Ray E. Lemley Expeditions, Part I. The Allingham Formation and a new Pleiocene vertebrate fauna from northern Australia. *Mem. Qd Mus.* **17**, 379-397.
- BAI ME, J. (1995) 30,000 years of fishery in western New South Wales. *Archaeol. Oceania*, **30**, 1-21.
- , MERRILLS, D. & PORTER, J. K. (1978) Late Quaternary mammal remains, spanning about 30,000 years from excavations in Devil's Lair, WA. *J. Roy. Soc. WA*, **61**, 33-65.
- BARTHOLOMAE, A. (1977) The fossil vertebrate fauna from Pleistocene deposits at Cement Hills, Gore, southeastern Queensland. *Mem. Qd Mus.* **18**, 41-51.
- (1978) The Macropodidae (Marsupialia) from the Allingham Formation, northern Queensland. Results of the Ray E. Lemley Expeditions, Part 2. *Ibid.* **18**, 127-143.
- (1979) New lizard-like reptiles from the Early Triassic of Queensland. *Alcheringa*, **3**, 225-234.
- BENNETT, G. (1875 [1876]) Notes on the *Chlamydosaurus* or frilled lizard of Queensland (*Chlamydosaurus kingii*) Gray, and the discovery of a fossil species on Darling Downs, Queensland. *Pap. Proc. Roy. Soc. Tas.* 56-58.
- BOLFS, W. E. & MACKNESS, B. S. (1994) Birds from the Bluff Downs Local Fauna, Allingham Formation, Queensland. *Rec. SA Mus.* **27**, 139-149.
- BOYDNER, S. (1974) An account of an archaeological reconnaissance of Hunter's Isles, north-west Tasmania. *Rec. Queen Victoria Mus.* **54**, 1-22.
- BROWN, G. W. (1991) Ecological feeding analysis of south-eastern Australian scincids (Reptilia: Lacertilia). *Aust. J. Zool.* **39**, 9-29.
- BUSTARD, R. (1968) The ecology of the Australian gecko *Heteromolia binoci* in northern New South Wales. *J. Zool. Syst. Lond.* **156**, 483-497.
- (1970) The population ecology of the Australian gekkonid lizard *Heteromolia binoci* in an exploited forest. *Ibid.* **162**, 31-42.
- COGGER, H. G. & HEATWOLF, H. (1981) The Australian reptiles: origins, biogeography, distribution patterns and island evolution pp. 133-137. In Keast, A. (Ed.) "Ecological biogeography of Australia [Monographiae Biologicae Vol. 41]" (Dr W. Junk, The Hague).
- COOK, D. L. (1960) Some animal remains found in caves near Margaret River, West. Aust. *Nat.* **7**, 107-108.
- (1963) The fossil vertebrate fauna of Strong's Cave, Boranup, Western Australia. *Ibid.* **7**, 153-162.
- CUNYAC-VILCH, J., COMPER, P., MOLNAR, R. E., WILLEN, G. & YONGE, B. (1990) Miocene dragons from Riversleigh: new data on the history of the family Agamidae (Reptilia: Squamata) in Australia. *Mem. Qd Mus.* **29**, 339-360.
- DOBSON, C. B. (1987) Aspects of the aquatic feeding ecology of the riparian skink, *Sphenomorphus spangli*. *Aust. J. Zool.* **35**, 253-258.
- DUNSON, J., FULLAGRA, R., FERBY, J., JONES, R. & PROSSER, J. (1993) Humans and megafauna in a late Pleistocene environment from Cuddie Springs, north western New South Wales. *Archaeol. Oceania*, **28**, 94-99.
- EUMMILL, A. G. (1969) Dentition pp. 117-200. In Gans, C. (Ed.) "Biology of the Reptilia" (Academic Press, London).
- ESTES, R. (1983) Sauria terrestrial. Amphisbaenia pp. 52-56. In Kubo, O. & Wellnhofer, P. (Eds) "Handbuch der Paläoherpetologie. Encyclopaedia of Palaeoherpetology Part 10A" (Gustav Fischer Verlag, Stuttgart).
- (1984) Fish, amphibians and reptiles from the Hadama Formation, Miocene of South Australia. *Aust. Zool.* **21**, 335-343.
- FOURNARY, G. J. III (1955) Further contributions to a monograph on the Megaloniidae and fossil Varanidae with notes on recent varanians. *Ann. Hist-Nat. Mus. Nat. Hung.* **29**, 1-128.
- FLANNERY, I. E. & RICH, T. H. (1981) Dinosaur digging in Victoria. *Aust. Nat. Hist.* **9**, 247-251.
- GODTHULA, H., ARCHER, M., GIBULLI, R., HAND, S. J. & GIBLISON, C. E. (1992) Earliest known Australian Tertiary mammal fauna. *Nature* **356**, 514-516.
- GRIFFIN, A. A. (1979) A phylogenetic subdivision of Australian scincoid lizards. *Rec. Aust. Mus.* **32**, 339-371.
- (1989) "The biology and evolution of Australian lizards" (Surrey Beatty & Sons, Chipping Norton).
- HALE, H. M. & TINDALE, N. B. (1930) Notes on some human remains in the lower Murray Valley, South Australia. *Rec. SA Mus.* **4**, 145-218.
- HAND, S. J., DAWSON, L. & ALGAR, M. (1988) *Macroderma kappi*, a new Tertiary species of false vampire bat (Microchiroptera: Megadermatidae) from Wellington Caves, New South Wales. *Rec. Aust. Mus.* **40**, 343-351.
- HECHT, M. (1975) The morphology and relationships of the largest known terrestrial lizard, *Megalania prisca* Owen, from the Pleistocene of Australia. *Proc. R. Soc. Vic.* **87**, 239-250.
- HOFFSTETTER, R. & GASC, J.-P. (1969) Vertebrae and ribs of modern reptiles pp. 201-310. In Gans, C. (Ed.) "Biology of the Reptilia" (Academic Press, London).
- HOPE, J. (1981) A goanna in the works. *Aust. Archaeol.* **12**, 115-122.
- , LAMPERT, R. J., EDMONDSON, E., SMITH, M. J. & VAN TETS, G. E. (1977) Late Pleistocene faunal remains from Seton rock shelter, Kangaroo Island, South Australia. *J. Biogeog.* **4**, 363-385.
- HORTON, D. R. (1972) Evolution of the genus *Egernia* (Lacertilia: Scincidae). *J. Herpetol.* **6**, 101-109.
- (1981) Faunal remains from the Early Man Rock Shelter pp. 35-44. In Rosenfeld, A., Horton, D. R. & Winter, J. W. (Eds) "Art and archaeology in the Laura area, north Queensland". *Terra Australis* Volume 6.
- HUTCHINSON, M. N. (1992) Origins of the Australian scincid lizards: a preliminary report on the skinks of Riversleigh. *The Bragle, Rec. NT Mus. Arts and Sciences* **9**, 61-69.
- (1997) The first fossil pygopod (Squamata, Gekkonota), and a review of mandibular variation in living species. *Mem. Qd Mus.* **41**, 355-366.
- & DONNELLAN, S. C. (1993) Biogeography and phylogeny of the Squamata pp. 210-220. In Glasby, C. J., Ross, G. J. B. & Beesley, P. L. (Eds) "Fauna of Australia, Vol. 2A. Amphibia and Reptilia" (Government Printing Service, Canberra).
- JAMES, C. D., LOSOS, J. B. & KING, D. R. (1992) Reproductive biology and diets of goannas (Reptilia: Varanidae) from Australia. *J. Herpetol.* **26**, 128-136.
- KING, D. & GREEN, B. (1979) Notes on diet and reproduction of the sand goanna, *Varanus gouldi-ruschebergi*. *Copeia* **1979**, 64-70.
- & — (1993a) "Goannas" (New South Wales University Press, Kensington).
- & — (1993b) Family Varanidae pp. 253-260. In Glasby, C. J., Ross, G. J. B. & Beesley, P. L. (Eds) "Fauna of Australia, Vol. 2A. Amphibia and Reptilia" (Government Printing Service, Canberra).
- KRETT, G. (1867) "Fossil remains of mammals, birds and reptiles from the caves of Wellington Valley" (Government Printer, Sydney).
- (1870) "Guide to the Australian fossil remains exhibited by the Trustees of the Australian Museum" (H. White, Sydney).
- (1871) "Australian Vertebrata - fossil and recent" (Government Printer, Sydney).
- LA DICK, T. C. (1991) Fossil snakes of Pit 91, Rancho La Brea, California. *Los Angeles City Mus. Contrib. Sci.* **424**, 1-28.

- LAMPERT, R. J. (1971) Burrill Lake and Currarong, Coastal sites in southern New South Wales. *Terra Australis* 1, 1-85.
- LOSOS, J. B. & GIBBENS, H. W. (1988) Ecological and evolutionary implications of diet in monitor lizards. *Biol. J. Linn. Soc.* 35, 379-407.
- MCDOWELL, S. B. & BOGERT, C. M. (1954) The systematic position of *Lanthanotus* and the affinities of the anguimorph lizards. *Bull. Am. Mus. Nat. Hist.* 105, 1-112.
- MACKNESS, B. S. (1995a) *Palonbestex selvstus*, a new species of palorchestrid from the early Pliocene Bluff Downs Local Fauna, northeastern Queensland. *Mem. Qld Mus.* 38, 603-609.
- (1995b) *Antonga malagurata*, a new pygmy darter from the early Pliocene Bluff Downs Local Fauna, northeastern Queensland. *Envir.* 95, 265-271.
- MARSHALL, L. G. (1973) Fossil vertebrate faunas from the Lake Victoria region, S.W. New South Wales, Australia. *Mem. Natl. Mus. Vict.* 34, 151-171.
- MEEUWS, R. (1942) Die Familie der Warane (Varanidae). *Abh. Senckenb. Naturforsch. Ges.* 462, 1-391.
- MOLNAR, R. E. (1978) Age of the Chillagoe crocodile. *Search* 9, 156-158.
- (1980) Australian late Mesozoic terrestrial tetrapods, some implications. *Mem. Soc. Géol. Fr.* 139, 131-143.
- (1982) Cenozoic fossil reptiles in Australia pp. 227-234. In Rich, P. V. & Thompson, E. M. (Eds) "The Fossil Vertebrate Record of Australasia" (Monash University Offset Printing Unit, Clayton).
- (1984a) Cenozoic reptiles from Australia (and some amphibians) pp. 337-341. In Archer, M. & Clayton, G. (Eds) "Vertebrate zoogeography and evolution in Australasia. Animals in space and time" (Hesperian Press, Carlisle).
- (1984b) A cheek-bist of Australian fossil reptiles pp. 405-406. *Ibid.*
- (1985) The history of lepidosaurs in Australia pp. 155-158. In Grigg, G., Shine, R. & Ehmann, H. (Eds) "Biology of Australasian frogs and reptiles" (Strey Beauty & Sons, Royal Zoological Society of New South Wales, Sydney).
- (1991) Fossil reptiles in Australia pp. 605-703. In Rich, P. V. & Thompson, E. M. (Eds) "The Fossil Vertebrate Record of Australasia" (Monash University Offset Printing Unit, Clayton).
- & CZECHURA, G. V. (1990) Putative Lower Cretaceous Australian lizard jaw likely a fish. *Mem. Qld Mus.* 29, 445-447.
- MOHRIG, C. (1983) Parthenogenesis in the endemic Australian lizard *Heteronotia binoci* (Gekkonidae). *Science* 220, 735-737.
- , DONOFFEN, S., ABAM, M. & BAYRSTOCK, P. R. (1989) The origin and evolution of parthenogenesis in *Heteronotia binoci* (Gekkonidae): extensive genotypic diversity among parthenogens. *Evolution* 45, 994-1003.
- MULHANNY, D. J. (1960) Archaeological excavations at Fromm's Landing on the lower Murray River, South Australia. *Proc. R. Soc. Vict.* 72, 53-85.
- , LAWSON, G. H. & TWITALE, C. R. (1964) Archaeological excavation of rock shelter No. 6 Fromm's Landing, South Australia. *Ibid.* 77, 479-516.
- PLIDGE, N. S. (1984) A new Miocene vertebrate faunal assemblage from the Lake Eyre Basin: a preliminary report. *Aust. Zool.* 21, 345-355.
- (1990) The upper fossil fauna of the Heuschke Fossil Cave, Naracoorte, South Australia. *Mem. Qld Mus.* 28, 247-262.
- (1992) The Curramulka local fauna: a late Tertiary fossil assemblage from Yorke Peninsula, South Australia. *The Beagle, Rev. NT Mus. Arts and Sciences.* 9, 115-142.
- RICH, P. V. & VAN TETS, G. E. (1982) Fossil birds of Australia and New Guinea: their biogeographic, phylogenetic and biostratigraphic input pp. 235-384. In Rich, P. V. & Thompson, E. M. (Eds) "The Fossil Vertebrate Record of Australasia" (Monash University Offset Printing Unit, Clayton).
- RICH, T. H., ARCHER, M., HAND, S. J., GODFREY, H., MURHEAD, J., PLIDGE, N. S., FLASHFORD, T. F., WOODBURN, M. O., CASE, J. A., TEDFORD, R. H., TURNBULL, W. D., FUNDELIUS, E. L. JR., RICH, L. S. V., WHITELAW, M. J., KEAD, A. & RICH, P. V. (1991) Australian Mesozoic and Tertiary terrestrial mammal localities pp. 1005-1057. *Ibid.*
- ROVER, A. S. (1956) "Osteology of the Reptiles" (University of Chicago Press, Chicago).
- RYDER, M. L. (1974) Report on the biological remains from Seelands Rock Shelter 1960 pp. 361-370. In McBryde, I. (Ed.) "Aboriginal prehistory in New England. An archaeological survey of north eastern New South Wales" (Sydney University Press, Sydney).
- SHEA, G. M. (1990) The genera *Tiliqua* and *Cyclodomorphus* (Lacertilia: Scincidae): generic diagnoses and systematic relationships. *Mem. Qld Mus.* 29, 495-520.
- & HUTCHINSON, M. N. (1992) A new species of lizard (*Tiliqua*) from the Miocene of Riversleigh, Queensland. *Ibid.* 32, 303-310.
- SKILBECK, C. G. (1980) A preliminary report on the late Cenozoic geology and fossil fauna of Bow, New South Wales. *Proc. Linn. Soc. N.S.W.* 104, 171-181.
- SMITH, M. A. (1982) Devon Downs reconsidered: changes in site use at a lower Murray Valley rockshelter. *Archaeol. Oceania* 17, 109-116.
- SMITH, M. J. (1976) Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia IV. Reptiles. *Trans. R. Soc. S. Aust.* 100, 39-51.
- (1982) Reptiles from Late Pleistocene deposits on Kangaroo Island, South Australia. *Ibid.* 106, 61-66.
- SPRING, E. C. (1889) List of donors and donations to the Museum during the year ending June 30th, 1889 pp. 13-15. In "Report of the Board of Governors of the Public Library, Museum and Art Gallery of South Australia, with the reports of the standing committees 1888-9" (Government Printer, Adelaide).
- STRON, R. A., TEDFORD, R. H. & WOODBURN, M. O. (1967) A new Tertiary formation and fauna from the Tiran Desert, South Australia. *Rev. SA Mus.* 15, 427-462.
- STORR, G. M. (1982) Revision of the bearded dragons (Lacertilia: Agamidae) of Western Australia with notes on the dismemberment of the genus *Amphibolmus*. *Rev. West Aust. Mus.* 10, 199-214.
- SUMIDA, S. S. & MURPHY, R. W. (1987) Form and function of the tooth crown structure in gekkonid lizards (Reptilia: Squamata, Gekkonidae). *Can. J. Zool.* 65, 2886-2892.
- TEDFORD, R. H. (1967) The fossil Macropodidae from Lake Menindee, New South Wales. *Univ. Calif. Publ. Geol. Sci.* 64, 1-156.
- THOMSON, S. A. & MACKNESS, B. S. (1999) Fossil turtles from the early Pliocene Bluff Downs Local Fauna, with a description of a new species of *Elseya*. *Trans. R. Soc. S. Aust.* 123, 101-105.
- THORNTON, A. G. (1971) The fauna pp. 45-47. In Wright, R. V. S. (Ed.) "Archaeology of the Gillies site, Koomaloo Cave". *Aust. Aboriginal Stud.* Volume 26.
- TINDALE, N. D. (1933) Tintalooma Caves, south-east of South Australia: geological and physiographic notes. *Trans. R. Soc. S. Aust.* 57, 130-142.

- TREZISE, J. (1970) Bone deposits in Chillagoe-Mungana Caves. *North Queens. Nat.* **37**, 2-4.
- WALTERS, I. N. (1980) Vertebrate remains from two sites on Moreton Island, Qld. *Aust. Archaeol.* **11**, 28-36.
- WILKINSON, J. (1995) Fossil record of a varanid from the Darling Downs, southeastern Queensland. *Mem. Qd Mus.* **38**, 92.
- WILLIAMS, D. L. G. (1980) Catalogue of Pleistocene vertebrate fossils and sites in South Australia. *Trans. R. Soc. S. Aust.* **104**, 101-115.
- WILLIS, P. M. A. & MACKNESS, B. S. (1996) *Quinkana babarra*, a new species of ziphodont mekosuchine crocodile from the early Pliocene Bluff Downs Local Fauna, northern Australia with a revision of the genus. *Proc. Linn. Soc. N.S.W.* **116**, 143-151.
- WITTEN, G. J. (1993) Family Agamidae pp. 240-252. In Glasby, C. J., Ross, G. J. B. & Beesley, P. L. (Eds) "Fauna of Australia. Vol. 2A Amphibia and Reptilia" (Government Printing Service, Canberra).
- WROE, S. & MACKNESS, B. S. (1999) Revision of the Pliocene dasyurid, *Dasyurus dunmalli* (Dasyuridae: Marsupialia). *Mem. Qd Mus.* **42**, 605-612.